

## Northern Sandplain Kwongan: effect of fire on *Hakea obliqua* and *Beaufortia elegans* population structure

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### Abstract

Individuals of obligatory reseedling species are killed outright by fires and species persistence in the Northern Sandplain shrubland ecosystem requires re-establishment by seed. *Hakea obliqua* and *Beaufortia elegans* share the same basic fire response syndrome—fire sensitivity of mature individuals, lack of seed dormancy and seed storage on the plant, but their adaptations relating to seedling establishment differ. *Hakea obliqua* has few but relatively large seeds and early seedling growth is rapid. *Beaufortia elegans* seedlings grow very slowly by comparison but continued existence in the shrubland ecosystems is ensured by the massive numbers of seed which are dispersed following fire. The massive, synchronous production of small seed apparently satiates seed harvesting predators and sufficient numbers of remaining seeds find conditions of the post-fire habitat favourable for re-establishment of the species.

Season of the burn had considerable impact on the re-establishment of these obligatory reseedling species. Seedling regeneration was most effective following autumn burns and least effective following spring fires. The implications for management in these Northern Sandplain shrublands are that ecologically unfavourable seasons (in this case, winter and spring) should be excluded from prescribed burning regimes if the objective of management is to maintain all components of the pre-fire ecosystem.

### Introduction

Fires in the Northern Sandplain shrublands play a major role in floristic structure of the vegetation (Bell and Loneragan 1985). Nearly one-third of the species in this region are killed outright by fire and rely on reseedling to maintain their position in these communities (Bell *et al.* 1984, Bell 1985, van der Moezel *et al.* 1987). Fire also plays an integral role in the reproductive biology of many plants in this environment by inducing synchronous flowering and seed production events (Gill 1981), causing seed release and dispersal (Cramer 1965a) and stimulating the germination of soil-stored seed (Purdie 1977).

The local post-fire persistence of obligate reseedling species is dependent on the events of seed dispersal, seed germination and seedling establishment. Seed store in these species can include both soil- and plant-borne propagules (Vlahos and Bell 1986). Fire stimulates the release of seed from bradysporous species (Cramer 1965b, Cowling and Lamont 1985) and the germination of soil-borne seed (Floyd 1976). Establishment is then dependent on the allocation of seed-stored nutrients and energy for early growth, acquisition of resources for subsequent growth, escape from insect and mammal predation, and survival in competition with other species of the habitat.

Seed contents and metabolic rates can effect establishment success. Northern sandplain shrubs present a range of seed sizes (Pate and Dell 1984) and early growth rates can vary enormously. Population densities following fire can also be strongly influenced by seed predators. Ants have been reported to collect up to 80% of the seeds shed following fire in stands of *Eucalyptus delegatensis* (Grose 1960, Cramer 1966). The massive, synchronized release of seed results in satiation of predators and subsequent seed escape (O'Dowd and Gill 1984).

This paper highlights the influence of fire on population densities in two obligatory reseedling species of the Northern Sandplain shrublands, *Hakea obliqua* R.Br. and *Beaufortia elegans* Schau.

### The species

*Hakea obliqua* (Proteaceae) is an erect shrub growing up to four metres tall in the deep sand shrublands of the region surrounding Badgingarra (Beard 1979). It has sharply pointed, terete leaves, 5–8 cm long and 3–4 mm thick. The flowers are white and are grouped in sessile axillary clusters along most of the length of the branches. The fruit is a woody structure measuring approximately 4x3x2 cm and covered by numerous corky outgrowths.

Two hemispherical seeds about 1 cm long and 0.5 cm thick are contained within each fruit capsule. The seeds have membranous wings and corky outgrowths on the convex side which is embedded in the fruit. Flowering generally occurs in early spring and begins when the plants are four years old (van der Moezel *et al.* 1987). Fruits start to accumulate on the plant from this age, remaining closed until opened by the effects of fire. The seeds are not dispersed immediately after fruit dehiscence but are generally held for up to two weeks by an attachment of the tip of the seed wing to the fruit.

The phanerocotylar seedlings (cotyledons exposed from the testa and borne at ground level upon germination) show moderate rates of early seedling growth (Delfs, unpublished data). By mid-October of the first growing season mean seedling weights average about 1 g plant<sup>-1</sup>. By two years plant weight has more than trebled and until at least 17 years both biomass and height increase linearly with age (Delfs *et al.* 1987). Plants of 17 years since last burn have mean biomass and height of 1440 g and 330 cm, respectively.

*Beaufortia elegans* (Myrtaceae) is much smaller at maturity in comparison, rarely exceeding 1 m in height (Delfs *et al.* 1987). The species has a dense crown of small (0.5 x 0.2 cm) leaves and pink clusters of flowers borne terminally. Flowering occurs in November and December (van der Moezel *et al.* 1987). Fruits are generally clustered together numbering 5-10 and measure approximately 0.5 x 0.5 cm. Seeds are numerous but small (0.45 g) and are enclosed in the fruit until burnt.

In contrast to *Hakea obliqua*, the seedlings of *Beaufortia elegans* are phaneroepigeal (exposed and elevated above the soil surface). The cotyledons are green and foliar (as are *Hakea obliqua*), but the hypocotyl is not nearly as elongated in *Beaufortia elegans*. The juvenile period in *Beaufortia elegans* is short despite its obligatory reseedling habit. Flowering occurs in less than two years following establishment (van der Moezel *et al.* 1987). Early seedling growth is very slow with seedlings of at least 15 weeks of age weighing less than 0.2 g or 1/40th of the weight of comparable aged *Hakea obliqua*. By two years mean plant weights average approximately 0.35 g and reach approximately 75 g after 17 years (vs 1440 g for 17 yr old *Hakea obliqua*) (Delfs *et al.* 1987).

### Methods

Population densities for *Hakea obliqua* and *Beaufortia elegans* were determined from a range of sites of known age since last burn in the vicinity of the junction of the Brand Highway and the Jurien Road (30°14'S, 115°16'E), approximately 20 km north of Badgingarra, Western Australia. Establishment of seedlings was determined in sites burned within the year prior to the winter seed germination period. Five adjoining 10 x 10 m stands burned the previous autumn and spring were sampled to establish the stand seed load of *Hakea obliqua* prior to burning. The number of seedlings established by August and the number of seedlings still surviving after two months growth were recorded. For *Beaufortia elegans* the number of seeds per plant was established from counts made on plants collected in five continuous one metre square quadrats. Seedling establishment density and two-month mortality figures were determined in two 1 m<sup>2</sup> quadrats.

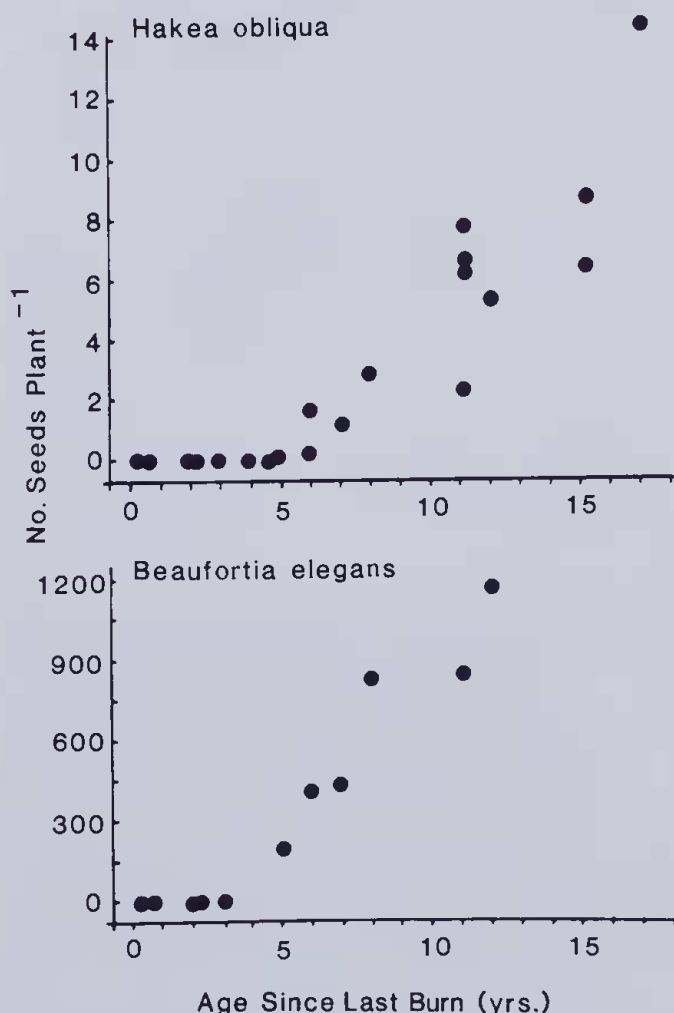


Figure 1.—Plant borne seed store in *Hakea obliqua* and *Beaufortia elegans* in Northern Sandplain shrublands of known age since last burn.

### Results

#### Seed store before fire

*Hakea obliqua* and *Beaufortia elegans* retain seed in protective fruits until released following death of the supportive tissue. Estimates of the seed store build-up following fire from the site of known age since last burn indicated that the large seeded species, *Hakea obliqua* produced far fewer seeds per plant than the small seeded species *Beaufortia elegans* (Fig. 1). Only the occasional plant of < 5 years held fruit in these two obligatory reseedling species. By about 11 years following fire the accumulated number of seeds per plant in *Hakea obliqua* averaged approximately 6 while the number of seeds stored in *Beaufortia elegans* plants of comparable age was more than 800.

#### Seedling recruitment following fire

Estimates of seed density prior to the burns and seedling density following fire indicate that *Hakea obliqua* re-establishes a higher proportion of available seed compared with *Beaufortia elegans* (Table 1). *Hakea obliqua* might be expected to establish approximately one seedling from seven plant-stored seed while *Beaufortia elegans* might be expected to establish only one in twelve. Seed freed from fruits by hand have high rates of germination (98% in *Hakea obliqua*, 96% in



Table 1

Population recruitment in *Hakea obliqua* and *Beaufortia elegans* from recently burned sites in the Northern Sandplain shrublands.

Species	Burn site	Age before fire	Adult plants pre-fire ha	Seeds pre fire ha	Seedlings post-fire ha	Percentage of seed establishment	Percentage of pre-fire population
<i>Hakea obliqua</i> .....	Autumn	>15	700	23 520	3 800	16	543
<i>Hakea obliqua</i> .....	Spring	11	3 640	6 400	860	13	24
<i>Beaufortia elegans</i> .....	Autumn	>15	28 000	29 600 000	2 354 000	8	8 407

*Beaufortia elegans*) (J.C. Delfs, unpubl.). Seed germination occurs within a week of imbibition and without artificial treatments (J.C. Delfs, unpubl.). Apparently large numbers of seed are predated between the time of the fire and the first significant rainfalls of late autumn and winter. The very much larger populations of *Beaufortia elegans* resulted from the much greater pre-fire density. In *Hakea obliqua* the recruitment of new seedlings was very much higher in the region burned in autumn only a few months prior to the winter rains. In the region burned the previous spring, however, the *Hakea obliqua* population was only one-fourth the density of the pre-fire condition.

In the interval between initial counts and density measurements after two months, little mortality had occurred. In two separate sites within the autumn burn, mortality was less than 10% in the first two months (Table 2).

Table 2

Seedling mortality of *Beaufortia elegans* in early months following establishment.

Site no	Adults pre-fire per m <sup>2</sup>	Seedlings post-fire	Survival after 2 months
1	8	1 491	97%
2	10	863	90%

## Discussion

### Species comparisons

Retention of seed on the plant until affected by fire is a strategy adopted by many species present in Australian plant communities (Gill 1981). Delayed dehiscence (bradyspory) is common in species from the families Proteaceae, Myrtaceae and Casuarinaceae (Gardner 1957, Specht *et al.* 1958). A fire is usually required for seed release but dehiscence may also occur when the woody fruit is dehydrated (Gill and Groves 1981). Species which retain seed until firing, such as *Hakea obliqua* and *Beaufortia elegans*, can exploit the open, well-lit, nutrient-rich, pyrogenic seed bed. Seeds accumulate on the plants during the inter fire period, then following post fire release and subsequent establishment ensure the survival of the species for the period until the next fire as both these species do not resprout following fire.

The comparatively large seed of *Hakea obliqua* germinates quickly following the first rain and growth is relatively rapid during the first growing season following fire. The proportion of seedlings surviving the first summer drought might be expected to be high in this species compared to the populations of the small seeded, slow growing *Beaufortia elegans*.

In California chaparral, moisture conditions in burned areas are less favourable than in unburned control areas (Christensen and Muller 1975). Also, mineral nutrient changes which accompany the fire have little or no effect

on post-fire germination responses but subsequent growth and survival on burned areas is thought to be enhanced by better nutrition and reduced grazing pressure. Summer conditions in the Northern Sandplains can be very dry, hot and windy; conditions most likely to be very detrimental to first-year seedlings. Seedlings which develop deep roots rapidly might be expected to have an advantage in preventing summer season dessication.

*Beaufortia elegans* appears to have opted for the production of very large numbers of seed of small size. This massive, synchronous reproductive event has possibly evolved in relation to seed predation. Ants predate or bury large numbers of seed (Briese and Macauley 1981). The large numbers of seed released into the habitat following fire results in satiation of predators and subsequent seed escape (O'Dowd and Gill 1984). Summer mortality might be expected to be comparatively greater due to the much smaller first-growing season size of *Beaufortia elegans* (Delfs *et al.* 1987). Although only 8% of the seed store of an area resulted in seedling establishment, less than 1% of the resulting germules would ultimately need to survive to replace the parent population.

Satiation of seed predators has been shown to be operative in the ultimate seed escape and germination of *Eucalyptus delegatensis* in the A.C.T. (O'Dowd and Gill 1984) and *E. incrassata* in north-western Victoria (Wellington and Noble 1985b). Successful post-fire population maintenance in *Beaufortia elegans* seems to rely on predator satiation and ultimately a safe site (*sensu* Harper 1977) where nutrients, light and moisture conditions are favourable to supplement the characteristically slow growth rate of this species.

Both *Hakea obliqua* and *Beaufortia elegans* share the same basic fire response syndrome-fire sensitivity in the adult, lack of prominent seed dormancy and seed storage on the plant. This adaptive strategy is advantageous when the fire frequency occurs at intervals longer than the primary juvenile period but shorter than the life span of the plant. *Beaufortia elegans* is capable of flowering in the second growing season while *Hakea obliqua* usually requires at least three full growing seasons before flowering in the fourth spring (van der Moezel *et al.* 1987). Plants in the site known to be at least 17 years since last burn were all vigorous indicating that the life span of both these species is probably considerably longer than 17 years. The natural frequency of burning in the Northern Sandplain shrublands is suspected to be of the order of 25 years (Bell 1985). Under the natural frequency of burning a significant buildup of plant-borne seed reserves would occur. Maintenance of population numbers would then depend on habitat conditions, especially in the first year following the fire.

In addition to the size of the seed reserves before episodic fires, the population dynamics of these species will also be highly dependent on rates of seed loss following dispersal and before germination and early

seedling mortality. Neither *Beaufortia elegans* or *Hakea obliqua* seed appeared to germinate in the region of the spring burn before the following winter. The seeds, generally dispersed in the first month following a fire, were, therefore, susceptible to seed predation for approximately 8 months prior to the first winter rainfalls. A considerable fire season difference in the proportion of *Hakea obliqua* seeds released which actually lead to established seedlings the following winter was observed. Seed predators are suspected of causing the reduced recruitment following the spring burn. Seed harvesting ants were the main cause of seed loss between dispersal and germination in *Eucalyptus incrassata*, a Victorian mallee with fire-induced seed fall (Wellington and Noble 1985a, 1985b). Seed predation was also the major cause of limited recruitment of South African bradydysporous species (Bond 1984).

#### Seedling mortality

Early mortality was minimal in *Beaufortia elegans* despite highly dense seedling stands. In Cape Province, South Africa, post-emergence seedling predation tends to be minimal in burned areas in contrast to areas of more mature shrubland where seedling predation can be very heavy (Bond 1984). This generalization also appears to apply to the Northern Sandplain. Seedling loss in shrubland habitats can be considerable. Several studies have documented high seedling losses in the first year or two after fire (Horton and Knaebel 1955, Hanes 1971, Wellington and Noble 1985a). The losses have most often been attributed to competition and drought stress (Schultz *et al.* 1955, Hanes 1977, Christensen and Muller 1975). Density independent mortality of seedlings of *Hakea obliqua* and *Beaufortia elegans* would tend to be high during the first drought season. Density dependent mortality might be expected later in the life cycle of these species. Senescence in these species due to factors related merely to age has not been observed in these species due to the lack of long unburned regions in the study area.

#### Season of burn

Season of burn appears to have a considerable impact on the continuing success of obligatory reseeding species in the Northern Sandplain. Seedling regeneration is most effective following autumn burns; least effective following spring burns. The seasonal differences are due: 1) to the length of time for predation of dormant seeds before the winter germination period and 2) mortality of seedlings due to the competitive advantage provided to the rapidly-resprouting species by the longer interval between the spring burn and germination compared to the autumn burn to winter germination interval. Winter and spring burns are clearly unfavourable for the maintenance of obligate reseeders in the shrublands of this region.

The implications for fire management of the Northern Sandplain and the problems that arise are fairly clear. If the objective of management is to maintain *all* the species present, it is imperative that the prescribed burning seasons should be strictly defined to exclude ecologically unfavourable seasons. Prescribed burning events can then be defined by the opportunity of suitable weather conditions in the ecologically favourable season. Aspects of the buildup of fire fuels are currently being studied (eg. Schneider and Bell 1985), however, fire behaviour studies in the Northern Sandplain shrublands should be a priority for future research. Until further knowledge of the reproductive strategies of shrubland species is documented a conservative path of fire

management should be followed (Hopper and Muir 1984). For the Northern Sandplain, late summer and autumn appear to be the ecologically most favourable season for prescribed burns. Fires during these seasons, however, have the potential to be uncontrollable and fire managers must be provided with guidelines for the safe limits under which prescribed burns may be conducted during these seasons.

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